Repeated downsweep vocalizations of the Araguaian river dolphin, *Inia araguaiensis*

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ABSTRACT

Araguaian botos (*I. araguaiaensis*) are known to produce pulsed as well as tonal sounds. Here, we present the first evidence for repetitive sequences of downsweep whistles in botos that appear to be shared between individuals and we investigate the context of their occurrence. Our study was conducted along the Tocantins River located in Eastern Amazon over a period of 42 days of boat surveys between 2012-2018. We observed 82 groups of Araguaian botos and acquired 43h of sound recordings. 632 downsweep whistles were recorded in 10 encounters. Four of these encounters contained downsweep bouts (21 bouts with ≥ 2 whistles) with short inter-call intervals (bout criterion 50s) and up to 161 whistles. We did not find a statistical relationship between downsweep occurrence and any of the contextual parameters we investigated including socializing, travelling, feeding, group size, presence of calves and socio-sexual displays. The rarity of these signals makes them unlikely candidates for individual or group identification. It is more likely that they are associated with very specific contexts such as nursing or mating, both of which were rarely observed in our study. Further studies are required to investigate context specificity and elucidate the function of these signals.

I. INTRODUCTION

All toothed whales (Odontoceti) produce pulsed calls for communication, with some species using these as their main social signals, e.g. orcas (*Orcinus* orca) (Ford, 1989; Deecke *et al*., 2010), northern right whale dolphins (*Lissodelphis borealis*) (Rankin *et al.*, 2007), narwhals (*Monodon monoceros*) (Marcoux *et al*., 2012), and pilot whales (*Globicephala* sp.) (Sayigh et al. 2013; Pérez *et* al. 2017). Pulsed calls are discrete signals composed of series of individual clicks (Schevill and Watkins, 1966). Such pulsed calls often encode social group identity (Deecke *et al*., 2010; Ford, 1989) but are also used in immediate social interactions such as conflict negotiation (Overstrom, 1983). Many marine dolphins (family Delphinidae) also use whistles in their social communication (Janik 2005; May-Collado *et al*., 2007). Whistles are defined as narrowband frequency modulated tonal sounds (Au *et al*., 2000; Richardson *et al*., 1995; Tyack, 2000). For most delphinids these sounds help to maintain cohesion of social groups (Janik and Slater, 1998; Janik 2005), and for some species such as the bottlenose dolphins (*Tursiops* sp.) whistles are also used to broadcast individual identity (Janik *et al*., 2006; Sayigh *et al*. 1999).

River dolphins are a polyphyletic group that is particularly interesting when studying acoustic communication in cetaceans because riverine habitats are very different from marine ones and may have led to changes in communication strategies. However, comparatively few studies exist on their vocalizations. Previous studies on the susu (*Platanista gangetica*) and the baiji (*Lipotes vexillifer*) were mainly conducted in captivity and therefore focused on very few individuals (Mizue *et al*., 1971; Wang *et al*., 1995, 1999; 2006; Xiao and Jing, 1989). Cremer *et al*. (2017) recently described the whistles and burst pulses of wild franciscana dolphins (*Pontoporia blainvillei*) and suggested that they might be used in mother-calf communication. The most commonly studied river dolphin is the boto (genus *Inia*) (Amorin *et al*., 2016; Caldwell *et al*., 1966; Diazgranados and Trujillo, 2002; May-Collado and

Wartzok, 2007; Ding *et al*., 1995, 2001; Kamminga *et al.*, 1993; Podos *et al*., 2002; Penner and Murchison, 1970). Initially they were thought to lack whistles in their repertoire (Podos *et al*., 2002) but later studies showed that whistles do occur, just not as often as pulsed sounds (May-Collado and Wartzok, 2007; Melo-Santos *et al*., 2019). The discrepancy in these results may be partly explained by geographic and genetic differences. For example, a recent study has discovered that botos in the Tocantins-Araguaia River Basin belong to a different species, the Araguaian boto (*Inia araguaiaensis*) than those found elsewhere (Hrbek *et al*. 2014).

Melo-Santos *et al.* (2019) described a variety of sounds produced by this new species, including whistles and pulsed calls. Araguaian boto calves were also found to produce bouts of short pulsed calls that were hypothesized to be contact calls for mother-calf communication (Melo-Santos, *et al*., 2019). Repetition introduces redundancy into a signal and thereby increases the probability of transmitting information successfully to a receiver.

Various animal groups produce repeated call sequences including birds (Catchpole and Slater, 2008), insects (Hedrick, 1986), frogs (Fellers, 1979) and terrestrial mammals (McComb, 1991). In cetaceans, rhythmically repeated calls have been reported for a wide range of species, such as the bottlenose dolphin (Jensen *et al*., 2012; Janik *et al*., 2013), short and long-finned pilot whales (*Globicephala macrorhynchus* and *Globicephala melas*, respectively) (Sayigh *et al*., 2013; Zwamborn and Whitehead, 2017); northern right whale dolphins (Rankin *et al.*, 2007), melon-headed whale (*Peponocephala electra*) (Kaplan *et al*., 2014), Guiana dolphins (Duarte de Figueiredo and Simão, 2009), humpback whales (*Megaptera novaeangliae*) (Payne and McVay, 1971), sperm whales (*Physeter macrocephalus*) (Watkins & Schevill 1977) and short-beaked common dolphins (*Delphinus delphis*) (Fearey *et al.*, 2019). Repetitive signals might work as mating calls (McComb, 1991; Smith *et al*., 2008), individual or group identifiers (Janik *et al*., 2013; Gero *et al*., 2016;

Zwamborn and Whitehead, 2017), mother-offspring contact (Smolker *et al*., 1993), territorial defense signals (Fellers, 1979), or even food calls (Janik, 2000). Here we present the first evidence for repetitive sequences of downsweep whistles in botos that appear to be shared between individuals and investigate the context of their occurrence.

II. METHODS

A. Study animals and area

Dolphins of the genus *Inia* are found in the Amazon, Orinoco and Tocantins river basins in South America (Best and Da Silva, 1989, 1993; Hrbek *et al*.; 2014; Santos *et al.*, 2012, 2014). These dolphins prefer slow flowing, sheltered waters with large concentrations of prey (Gomez-Salazar *et al*., 2012b; Martin *et al*., 2004; Pavanato *et al*., 2016). They are usually solitary or in mother-and-calf pairs. Larger aggregations are formed for mating and to feed on large schools of fish (Best and Da Silva, 1989, 1993; Gomez-Salazar *et al.*, 2012a; Martin *et al.*, 2008).

Our study was conducted along the Tocantins River located in the Eastern portion of the Amazon (Fig. 1). This river is characterized by clear waters, sandbanks, herbaceous and floating vegetation, and aquatic macrophytes in areas with light penetration (Junk *et al.*, 2011). The greatest rainfall occurs from November to April, the lowest waters are in September and the highest in March (Ribeiro *et al.*, 1995). The lower Tocantins River comprises the area between the mouth of the river and the city of Tucuruí, where there is deposition of sediments and floodplains (Goulding *et al.*, 2003; Ribeiro *et al*., 1995; Santos and Jégu, 1989). The area upstream of the Tucuruí dam is known as middle Tocantins River (Goulding *et al.*, 2003; Ribeiro *et al*., 1995; Santos *et al*., 1989). The Tocantins river is heavily impacted by human activities in its vicinity such as the operations of large cities and farms along the banks, fishing, the use of water for irrigation and electrical power generation,

116 the operation of vessels for transport and fishing and the refinement of ore (Goulding *et al.*,
117 2003; Ribeiro *et al*. 1995).
118
119 B. **Data collection**
120 We conducted 42 days of boat surveys from June 2012 to January 2018. Surveys were
121 conducted around the Capim Island (01°33'48.43"S 48°50'37.81"W) in the mouth of the
122 Tocantins River and between the cities of Baião (02°38'57.26"S 49°40'44.94"W) and Marabá
123 (05°19'21.02"S 49°7'29.02"W), including the reservoir of the Tucuruí Hydroelectric Plant
124 (Fig. 1, Table I). Around the Capim Island we used a 7m wooden boat with a 2-stroke center
125 engine and for the rest of surveys we used a 10m aluminum boat with 40 horsepower 4-stroke
126 outboard engine. During surveys we maintained a boat speed between 5.4-8.1 knots in an
127 area up to 200m from shore. *Inia* dolphins prefer these shallow areas most likely due to
128 increased prey density (Gomez-Salazar *et al*., 2012a; Pavanato *et al*., 2016). When possible,
129 we crossed the river once every 10km to include animals in the middle of the river channel in
130 our recordings.
131 When a group of dolphins was sighted, we reduced speed, shut the engine off and
132 began recording when we were approximately 20-50m from the animals. Recording sessions
133 lasted between 2.53 minutes to 2.3 hours; recording time depended on our ability to track the
134 animals. If a group avoided the boat approach three times we proceeded searching for another
135 group. In 2012 and 2013 we used an Aquarian Hydrophone System connected to a Tascam
136 DR-1 recorder, sampling rate 44kHz. In 2017 and 2018 we recorded dolphins using a High
137 Frequency Soundtrap (Oceans Instruments), sampling rate 576 kHz. During recordings we
138 took notes on group size and age composition, behavior, habitat, geographical position, and
139 river state (0 to 3 in an increasing scale of turbulence). Behavioral sampling of aerial
140 behavior followed the continuous *all event* method (Altman, 1974). A group was defined as

141 animals in a radius of 100m from each other; we watched continuously over group size and
142 composition and took note on the highest number of animals for each encounter. We
143 considered calves as those animals with less than half the size of an adult, also recognizable
144 by their stunted rostrum. Habitat types were classified according to Gomez-Salazar *et al*.
145 (2012a) and Pavanato *et al*. (2016) as follows: main river channel, channel, island, main river
146 margin, lake, streams, and rocky formations. Behavioral states were categorized as: 1)
147 travelling: unidirectional movement in any speed; 2) socializing: frequent body contact
148 between animals and surface displays (*e.g.* leaps, object-carrying) and 3) feeding: repeated
149 diving in the same area, surfacing in multiple directions and diving with an arched dorsum.
150 As botos are normally slow swimmers (Best & Da Silva 1989, 1993) and the animals we
151 observed were always in motion we did not include a resting category.
152
153 **C. Acoustic and statistical analyses**

154 We defined downsweeps as tonal signals with initial frequency higher than the final
155 frequency and no inflection points. Inflection points were defined as a point where the slope
156 of the whistle contour reverses direction (Au *et al*., 2000). Acoustic analysis was carried out
157 in the software Luscinia (https://github.com/rflachlan/Luscinia/wiki). We identified
158 downsweeps with high signal-to-noise ratio, traced their contours and extracted the following
159 parameters: fundamental frequency, peak frequency, duration, Wiener entropy and
160 harmonicity. The last two parameters were added as measurements of noisiness, because
161 sounds produced by *Inia* dolphins have, sometimes, noisy components. Then, we used a
162 dynamic-time warping algorithm to compare the measured parameters between calls. This
163 technique allows for extension and compression of a signal along the time axis, ensuring
164 maximum overlapping of the frequency domain when comparing two signals (Buck and
165 Tyack, 1993; Deecke and Janik, 2006; Sakoe and Chiba, 1978). The resulting dissimilarity

matrix from the time-warping analysis was converted to Euclidean distances for further statistical analysis. We then ran a non-metric multidimensional scaling analysis (NMDS). The dimensions of the NMDS were used in a principal component analysis (PCA) for further data reduction. The results were plotted to visualize differences in downsweeps produced by different groups and populations. Inter-call intervals and downsweep parameters were measured in Raven Pro 1.5 (Cornell Laboratory of Ornithology, New York, NY, USA. Downsweep whistle bouts with an inter-whistle interval shorter than 0.05s were excluded from the analysis, as it appeared that they were produced by more than one individual as indicated by occasional overlap of whistles in such bouts (112 downsweep whistles in five bouts excluded).

To investigate the behavioral context of *Inia* downsweeps, we modelled the presence and absence of downsweeps in each recording session using a generalized linear model (GLM) (logit link, binomial family):

$$\left(\overline{D}\right) = \frac{\exp\left(\beta_0 + \beta_1\phi_s + \beta_2\phi_t + \beta_3 c + \beta_4 g + \beta_5 r\right)}{1 + \exp\left(\beta_0 + \beta_1\phi_s + \beta_2\phi_t + \beta_3 c + \beta_4 g + \beta_5 r\right)} \qquad D \sim Binomial(\overline{D})$$

where D represents the probability of one or more downsweeps being produced in a recording session and $\overline{D}$ represents expected probabilities. Parameters β_1 and β_2 represent the difference in model intercept (β_0) when dolphins were socializing (ϕ_s) or travelling (ϕ_t), relative to feeding. The effects of the number of calves present (c) and group size (g) are represented by β_3 and β_4, respectively. Because our ability to record dolphin sounds varied across behavioral state, some states were associated with longer recording durations than others (e.g. socializing mean = 65.63 min ± 8.06 and feeding mean = 28.46 min ± 3.84). Expecting that a call type should be more likely to be detected with longer recording samples,

we simultaneously estimated β_5, the effect of recording duration (r, mins) to avoid confounding the effects of behavior on downsweep production.

Next, to investigate possible relationships between downsweep production and discrete behavioral events, we fit the following GLM (logit link, binomial family):

$$(\overline{D}) = \frac{exp(\varepsilon_0 + \varepsilon_1\phi_b + \varepsilon_2\phi_f + \varepsilon_3\phi_l + \varepsilon_4\phi_o + \varepsilon_5\phi_p + \varepsilon_6\phi_s + \varepsilon_7\phi_t + \varepsilon_8 r)}{1 + exp(\varepsilon_0 + \varepsilon_1\phi_b + \varepsilon_2\phi_f + \varepsilon_3\phi_l + \varepsilon_4\phi_o + \varepsilon_5\phi_p + \varepsilon_6\phi_s + \varepsilon_7\phi_t + \varepsilon_8 r)}$$

$$D \sim Binomial(\overline{D})$$

where parameters ε_1, ε_2… through ε_7 represent the difference in expected probability of a downsweep being produced in a given recording session ($\overline{D}$) when "body contact", "flippers, fluke and belly exhibitions", "leaps", "object-carrying", "penis exhibitions", "synchronized leaps", or "tail slaps" occurred, respectively, and ε_8 represents the effect of recording duration (r, mins) (See Table II for descriptions of discrete behavior patterns). Both of the above models were also run as a quasi-binomial model to test for overdispersion. All statistical analyses were conducted using R 3.4.2 (R Core Team 2017).

In order to define downsweep bouts we used a log survivorship analysis as described by Slater and Lester (1982). We present inter-whistle intervals within bouts as well as between bouts and single downsweep emissions.

III. RESULTS

We encountered 82 groups of Araguaian botos, comprising sightings of 385 individuals. Group size varied from 1 to 20 animals (mean= 5±0.5). Calves were present in 28 groups. We analyzed 43 hours of sound recordings from these sightings, identifying 632 downsweeps in recordings from 10 groups; calves were observed in seven of these groups.

The minimum number of downsweeps in an encounter was one and the maximum was 287 (Table III, Fig. 2). Downsweeps were often produced in bouts with short inter-call intervals. We used 50 s as a bout inter-whistle interval criterion determined by log analysis of the distribution of inter-whistle intervals (Slater and Lester, 1982). We found 21 bouts with the shortest bout consisting of only 2 whistles and the longest of 161 whistles (median=9 whistles, 25% quantile=3, 75% quantile=25). Inter-whistle intervals within bouts ranged from 0.052 to 45.82 s (median=1.01, 25% quantile=0.71, 75% quantile=2.37). Intervals between bouts or single downsweep emissions varied from 51.12 to 1901.65 s (median=164.89, 25% quantile=75.51, 75% quantile=317.20) (Fig. 3, Table III). Among the 82 groups we observed in our study, three displayed social-sexual behavior (calves present in all these observations), which included object-carrying, exhibition of the penis and close body contact between individuals. Of these three groups, two emitted downsweep bouts.

Table III summarises downsweep whistle parameters. In the principal component analysis, the first principal component explained 68.2% of the variance in the downsweep parameters and the second principal component explained 14.9% of the variance. While there was no clear differentiation between populations (lower and middle Tocantins River), two groups, one from each population, produced very characteristic signals and formed tight clusters on the ordination analysis (Fig. 4).

To investigate the context of downsweep whistling, we conducted GLM analyses. We were unable to confidently identify a behavioral state for three of 82 recordings, as the animals were only observed on the surface once. These recordings were excluded from the GLMs. There was no evidence of overdispersion in either the quasi-binomial behavioral state GLM (overdispersion parameter = 0.99) or the discrete-event GLM (overdispersion parameter = 1.32). Thus, we interpreted parameter estimates from the models of the binomial family. Relative to feeding (the background behavioral state in our model), downsweeps were

estimated to be more likely to occur when animals were traveling or socializing, though these estimates were associated with large standard errors and were not statistically significant (Table IV). The presence of calves was also included in the analysis but again no significant relationship with downsweep production was discovered. Downsweeps were significantly more likely to be detected in long recordings, suggesting that sampling duration was more influential than the behavioral and group measures we included. Similarly, we found that none of the discrete behavioral events that we analyzed had a significant effect on the occurrence of downsweeps (Table V).

IV. DISCUSSION

Downsweep whistles of Araguaian botos were often produced in long bouts with short inter-call intervals. All bouts occurred in social or feeding groups with the presence of calves (Table III). However, these sounds were generally rare. They were identified during only 10 of 82 *Inia* encounters, which comprised over 43 hours of recordings across a wide variety of behavioral contexts and locations. Furthermore, downsweeps were not detected by Melo-Santos *et al.* (2019) in 15 hours of recordings of a socializing/feeding group of human-habituated dolphins in the lower reaches of the Tocantins River. This suggests such sounds are used in more specific behavioral contexts. Nevertheless, our GLMs do not show statistically significant relationship between the emission of downsweeps and behavioral state and/or discrete behavioral events. The occurrence of bouts was correlated with long recording sessions, which might be related to the fact that foraging and socializing groups of *Inia* were easier to track since they tended to stay in the same area for longer periods when engaged in these behaviors.

Downsweeps have been documented across several species of cetaceans: botos (*Inia geoffrensis*) (May-Collado and Wartzok, 2007); Guiana dolphins *Sotalia guianensis* and tucuxis (*Sotalia fluviatilis*) (Melo-Santos, 2018; Pivari and Rosso, 2005); pilot whales (*Globicephala macrorhynchus* and *Globicephala melas*) (Dreher and Evans, 1964; Taruski, 1979); *Stenella longirostris* (Bazúa-Durán and Au; 2002); common dolphins (*Delphinus* sp.) (Dreher and Evans, 1964; Ansmann *et al*., 2007; Petrella *et al.*, 2012); bottlenose dolphin (*Tursiops truncatus*) (Dreher and Evans, 1964; Janik *et al*. 1994; Janik and Slater, 1998); orcas (*Orcinus orca*) (Filatova *et a*., 2012; Simonis *et al.*, 2012; Samarra *et al*., 2015); humpback dolphins (*Sousa chinensis*) (Van Parijs and Corkeron, 2001); franciscanas (*Pontoporia blainvillei*) (Cremer *et al.*, 2017) and belugas (*Delphinapterus leucas*) (Garland *et al.*, 2015). Among these studies Garland *et al.* (2015), May-Collado and Wartzok (2007) and Petrella *et al*. (2012) and Samarra *et al*. (2015), reported downsweeps as the most common whistle type found in their samples. However, none of the above studies report downsweeps being used in a repetitive fashion or identify the contexts in which these signals were used. The exception is Dreher and Evans (1964) who reported that three juvenile bottlenose dolphins produced downsweeps in rapid repetition in situations of stress or fright. Our surface observations did not suggest that dolphins were in stress or frightful situation (e.g. aggressive behavior) when downsweep bouts were produced. However, we cannot account for behavior of dolphins whilst submerged. Simonis *et al*. (2012) also noted the repetitive use of downsweep sounds by orcas, and because of their similarities to bat echolocation calls these authors suggested that orcas might use series of downsweeps for echolocation. The downsweeps we recorded were much lower in frequency and clicks were present continuously in all of our recordings, suggesting it is unlikely downsweeps serve as echolocation sounds. Moreover, if *Inia* downsweeps were used for echolocation one would expect them to be more common, since echolocation is vital for Inia navigation and

289 orientatione. May-Collado and Wartzok (2007) suggested that botos use whistles primarily to
290 maintain inter-individual distance. Our observations of botos producing downsweep bouts
291 during social and foraging activities with synchronized surface behavior suggests that this
292 might not be the case for Araguaian botos. Further support for such a functional difference
293 comes from the fact that downsweeps presented in May-Collado and Wartzok (2007) for
294 botos (*I. geoffrensis*) in the Napo River (Ecuador) appeared to have different frequency
295 contours of those recorded in our study.

296 Cetaceans often use repeated sequences of sounds to broadcast their individual or
297 group identity (Janik *et al*., 2013; Gero *et al*., 2016; Sayigh *et al*., 2013). Identity is conveyed
298 by the patterns of frequency modulation of sounds (Janik *et al*., 2006) or through the order in
299 which pulses are repeated (Watkins and Schevill, 1977). As boto downsweeps have relatively
300 simple contours (Figure 2) it is unlikely that they serve as individual identifiers in this way.
301 However, two groups produced bouts of distinct downsweeps, suggesting possible group
302 specificity. Nevertheless, their rare occurrence in our recordings makes it unlikely that they
303 are required to maintain group cohesion as in delphinids (Janik, 2009). More common signals
304 like pulsed calls (Melo Santos *et al*., 2019) likely play a more important role in social
305 cohesion than downsweeps.

306 Given that downsweep emissions often occurred in long bouts (Figure 3), and these
307 bouts always occurred in the presence of calves, it is possible that they could function as
308 begging calls (Godfray 1995a, 1995b). Animal begging calls are normally produced by
309 infants demanding resources (often food) from their parents (Godfray 1995a, 1995b; Manser
310 *et al*. 2008). In cetaceans, sounds occurring before suckling have been recorded for
311 humpback whales (*Megaptera novaeangliae*), however mechanical cues are more important
312 to initiate nursing (Videsen *et al*. 2017). Sounds associated with suckling were also reported
313 for captive neonate bottlenose dolphins (Morisaka *et al*., 2005). In botos, sound bouts,

especially whistles, might be important to start nursing. However, we did not detect a significant statistical relationship between the presence of calves and the production of downsweeps, possibly due to the small number of observations in our study.

In 2 out of 5 encounters with downsweep bouts, we also noticed surface displays which might indicate socio-sexual behavior such as object-carrying, exhibition of penis, and close contact between individuals. Mating calls of other animal species are also produced in bouts so as to attract the attention of possible mating partners, and this behavior if spread over a variety of taxa including insects, amphibians, birds and mammals (Catchpole and Slater, 2008; Fellers, 1979; Hedrick, 1986; Reby and Charlton, 2012). It is possible that Araguaian boto downsweeps have a similar function in the context of mating. Both downsweep production and social-sexual behavior are not observed very often which makes this a difficult relationship to study. Future studies should aim to localize sounds to individuals to help with the identification of calling contexts.

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576 TABLE I. Summary of surveying effort along the Tocantins River.

Location	Month	Year	Number of surveying days
Capim Island	June	2012	1
	July	2013	3
Baião-Marabá	September	2017	20
	January	2018	18

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578

579 TABLE II. Definition of discrete behavioral events

Behavioral event	Definition
Body contact	Animals touching each other's bodies
Flippers, fluke and belly exhibitions	Dolphins swimming sideways or belly-up so that the flippers, belly and/or fluke are shown above the water surface
Leap	Single animal jumps out of the water exhibiting most of its body
Synchronized leap	Two or more dolphins jump out of the water exhibiting most of their bodies
Object-carrying	Dolphin holding an object (e.g. pebble, vegetation) with its rostrum out of the water
Penis exhibition	Animal swimming belly-up and exhibiting its penis out of water
Tail slap	Dolphin slapping its tail fluke on the water surface one or multiple times

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581

582 TABLE III. Characterization of all downsweep whistles. The “L” in Group ID indicates animals recorded in the Lower Tocantins River, while
583 the “M” stands for recordings of the Middle Tocantins River. Encounters where we detected downsweep bouts have their Group ID in bold.
584 Mean and standard error are presented for acoustic parameters of downsweeps.

Group ID	Behavioral state	Group size	Number of calves	Recording time (min)	Number of downsweeps	Duration (sec±SE)	Minimum frequency (kHz±SE)	Maximum frequency (kHz±SE)	Frequency range (kHz±SE)	Peak frequency (kHz±SE)
L1	Feeding	5	1	33.48	161	0.06±0.001	5.661±0.069	16.98±0.13	11.32±0.13	7.04±0.18
L2	Traveling	2	0	4.37	1	0.04	7.27	11.24	3.97	8.58
L3	Socializing	6	1	52.15	44	0.04±0.005	3.52±0.15	5.45±0.16	1.93±0.12	3.97±0.16
M1	Socializing	18	1	138.5	131	0.042±0.002	3.83±0.08	6.09±0.16	2.64±0.12	4.63±0.09
M2	Feeding	8	2	118.15	4	0.03±0.002	3.53±0.51	5.25±1.01	1.72±0.63	3.90±0.44
M3	Socializing	15	1	87.36	287	0.07±0.001	9.19±0.04	13.67±0.05	4.48±0.06	9.95±0.05
M4	Feeding	2	0	18.02	1	0.07	2.66	4.80	2.13	3.37
M5	Socializing	3	0	56.26	1	0.09	8.02	20.42	12.40	8.86
M6	Feeding	8	1	56.85	1	0.02	11.65	17.13	5.48	11.95
M7	Feeding	4	1	125.9	1	0.05	9.20	14.05	4.84	13.08
Total		71	8	691.04	632	0.06±0.001	6.73±0.10	12.32±0.17	5.58±0.14	7.64±0.10

585

586 TABLE IV. Estimated parameters relating the presence of downsweep vocalizations in
587 recordings of *Inia* to behavioral context and group characteristics. Relationships were
588 estimated with a generalized linear model (binomial family, logit-link).

	Estimate	SE	*z*	*p*
Intercept	-3.737	0.875	-4.270	< 0.001
Behavior: Socializing	1.310	0.898	1.458	0.145
Behavior: Travelling	1.426	1.353	1.054	0.292
Number of calves	0.525	0.771	0.682	0.495
Group size	-0.149	0.111	-1.344	0.179
Recording duration	0.0412	0.018	2.330	0.020

589

590

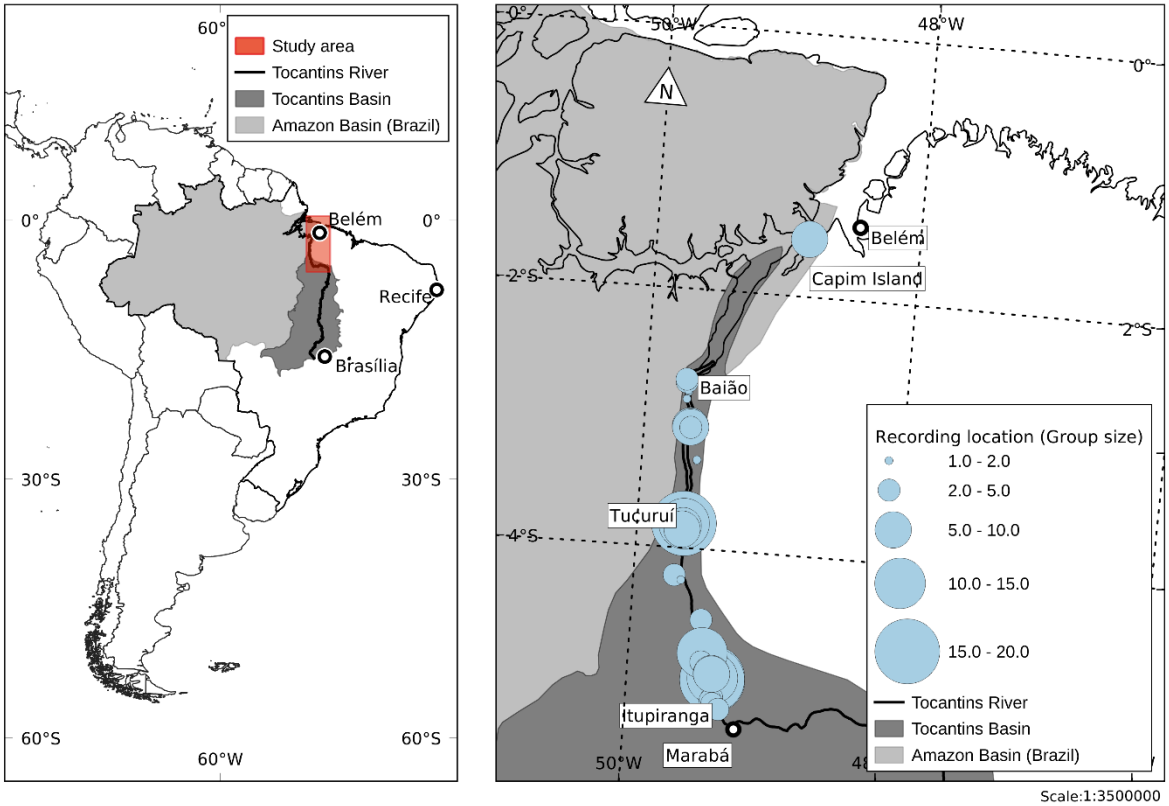
591 TABLE V. Estimated parameters relating the presence of downsweep vocalizations in
592 recordings of *Inia* to discrete behavioral events. Relationships were estimated with a
593 generalized linear model (binomial family, logit-link).

	Estimate	SE	*z*	*p*
Intercept	-3.746	0.817	-4.585	< 0.001
Body contact	0.014	1.257	0.011	0991
Flippers on belly	0.761	1.255	0.606	0.544
Leap	0.950	1.043	0.911	0.362
Object carrying	-0.249	1.799	-0.138	0.890
Penis exhibition	17.529	2399.545	0.007	0.994
Synchronized leap	-0.225	1.367	-0.165	0.869
Tail slap	-0.427	1.412	-0.302	0.763
Recording duration	0.025	0.014	1.801	0.072

594

595

596 **COLLECTED FIGURE CAPTIONS**



597

598 FIG. 1**.** Location of study area and of sound recordings of Araguaian botos, *Inia*

599 *araguaiaensis*, in the Tocantins River.

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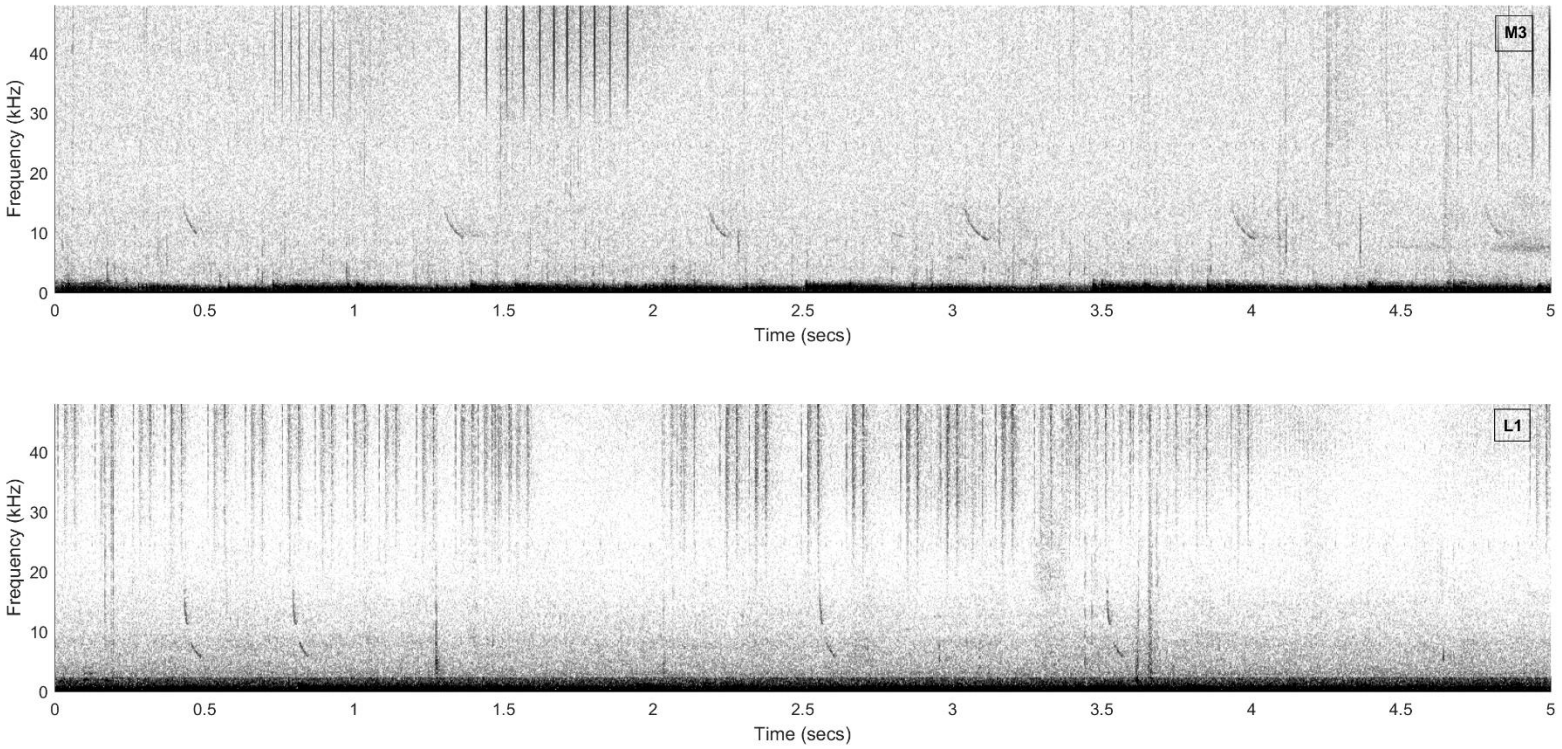


603

604 FIG. 2. Examples of downsweeps produced by Araguaian botos in the Tocantins River. Labels in the spectrograms indicate the group of botos
605 from which the sound recording is represented. The “L” in Group ID indicates animals recorded in the Lower Tocantins River, while the
606 “M” stands for recordings of the Middle Tocantins River.

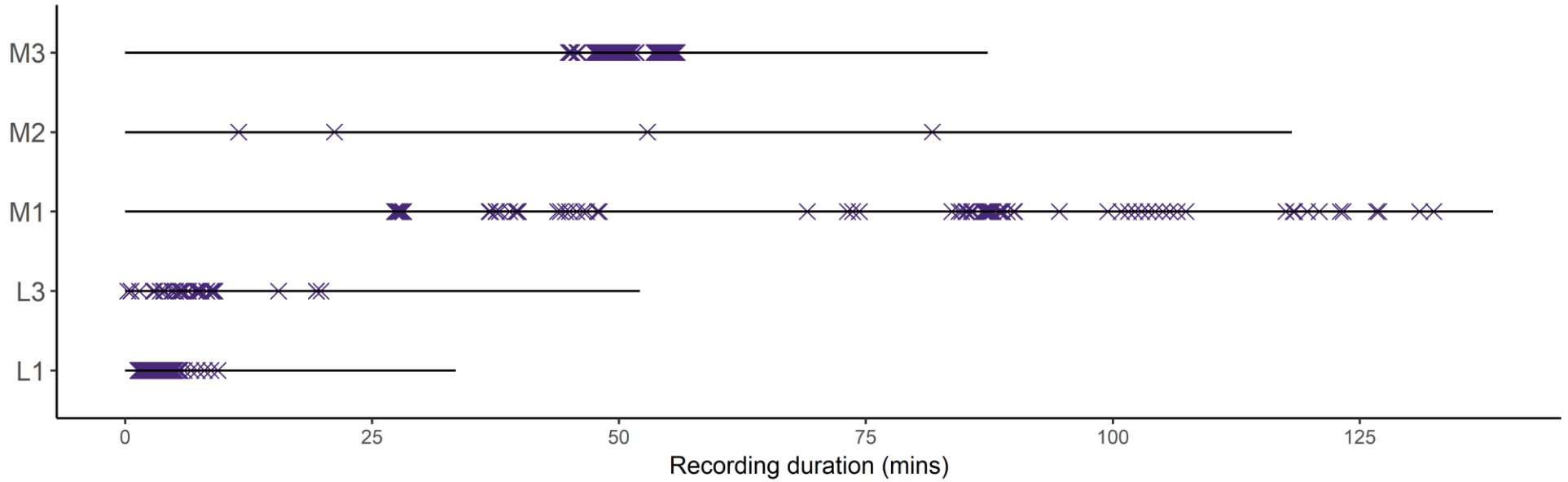
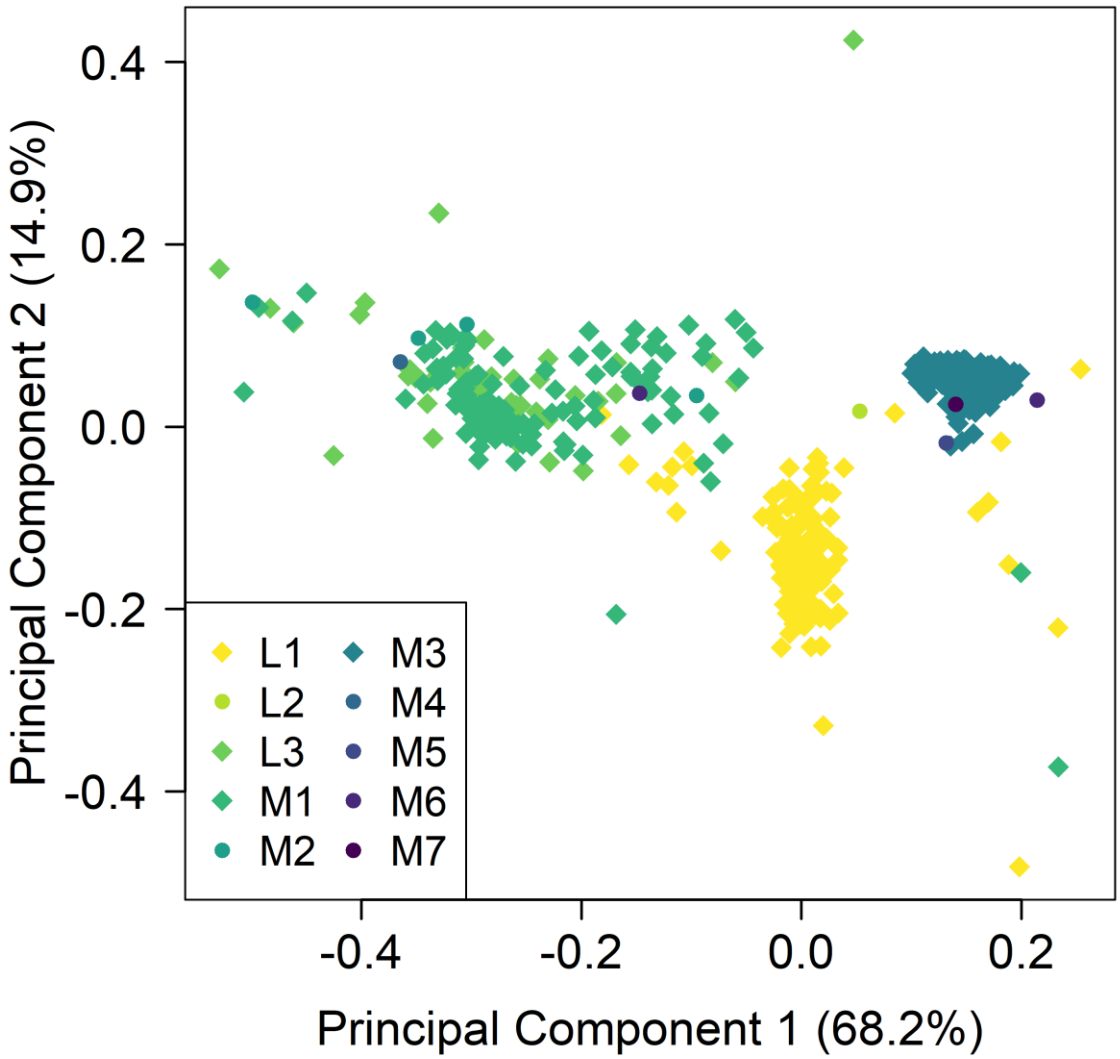


FIG. 3. Distribution of downsweeps within each recording session. Purple X's represent downsweep emissions and the continuous lines represent the recording time for each group of Araguaian botos.



611

612 FIG. 4. Visualization of downsweep characteristics in multivariate space according to two
613 components in a PCA. Colours and shades indicate recording sessions. The “L” in
614 Group ID indicates animals recorded in the Lower Tocantins River, while the “M”
615 stands for recordings of the Middle Tocantins River.